Biological invasion threatens keystone species indelibly entwined with Indigenous cultures

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Black ash (*Fraxinus nigra*), the most highly preferred and vulnerable host of the invasive emerald ash borer (EAB; *Agrilus planipennis*) in North America, is of cultural and spiritual importance to many Tribal Nations in the US and First Nations in Canada. To date, EAB has invaded nearly 60% of the native range of black ash, with annual spread averaging approximately 50 km per year. On the basis of the predicted expansion of EAB distribution, we estimate that more than 75% of black ash basal area will be lost across 87% of the species' North American range by 2035. Census data indicate that 98% of Indigenous people currently residing within the geographic range of black ash in the US will be within the area experiencing more than 75% basal area loss by 2035, suggesting broad and multidimensional impacts of EAB invasion for those who value black ash as a cultural keystone species. Collaborative efforts among scientists, resource managers, and Indigenous experts are needed to mitigate EAB impacts and preserve or protect black ash resources, given the species' vulnerability to EAB and its associated cultural and ecological value.

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The native range of black ash (*Fraxinus nigra*), an ecologically unique, foundational wetland species, extends through the northern states of the eastern US and the southern provinces in eastern Canada (WebFigure 1). Although black ash occurs in mixed-species mesic forests, it is notably abundant in swamps, floodplains, and riparian forests. In these systems, slow-growing black ash trees regulate hydrological processes and nutrient dynamics, as well as provide vertical structure, habitat, and food for many organisms; in addition, the senescent leaves of black ash represent a high-quality annual nutrient input (Youngquist *et al*. 2017; Klooster *et al*. 2018; Kolka *et al*. 2018).

Black ash is also a cultural keystone species for dozens of Tribal Nations in the US and First Nations in Canada (Figure 1), prominently featured in the origin stories and ceremonial practices of several tribes and valued as a source of traditional medicines (Benedict and David 2000; Garibaldi and Turner 2004; COSEWIC 2018). Generations of Indigenous basketmakers have carefully selected, harvested, and debarked individual black ash trees. Logs are pounded until growth rings separate, yielding thin pliable splints that are woven into artistic and utilitarian baskets (Benedict 2001; Willow 2011). Although some Native American Tribal lands contain forests with a black ash component, many basketmakers harvest trees in federal, state, or private forests with special permits or landowner permission.

However, black ash is also both a highly preferred host and the most vulnerable ash species encountered to date by emerald ash borer (EAB; *Agrilus planipennis*), which has become the most destructive forest insect to invade North America (Aukema *et al*. 2011; Herms and McCullough 2014). Native to Asia, EAB was first discovered in 2002 in southeast Michigan and southern Ontario (Cappaert *et al*. 2005; Siegert *et al*. 2014a), a region that corresponds to the longitudinal mid-range of black ash. EAB larvae feed on phloem in serpentine galleries, and also typically score the outer xylem. As larval densities increase, galleries disrupt nutrient and water transport, causing branches and eventually entire trees to die. Moreover, because individual galleries often extend further horizontally in black ash, mortality typically occurs at lower larval densities than in other ash species (McCullough 2019). Recent surveys have shown complete or near-complete mortality of overstory black ash following EAB invasion (DGM and NWS unpublished data; Engelken and McCullough 2020; Siegert *et al*. 2021). Regeneration varies; black ash seed years occur irregularly at intervals of up to 8 years (Erdmann *et al*. 1987), while viable root or stump sprouts are rare on trees killed by EAB (Engelken and McCullough 2020; Siegert *et al*. 2021). Given persistent endemic EAB populations and (in some areas) competition from other mesic-adapted tree species, the likelihood that existing black ash saplings or seedlings will survive to maturation and seed production is tenuous.

Notably high rates of black ash mortality following EAB invasion have alarmed basketmakers and other Indigenous peoples whose long-standing cultural ties to black ash may be at risk. Using the expanding footprint of the EAB infestation as a proxy, we projected EAB spread across the native range of

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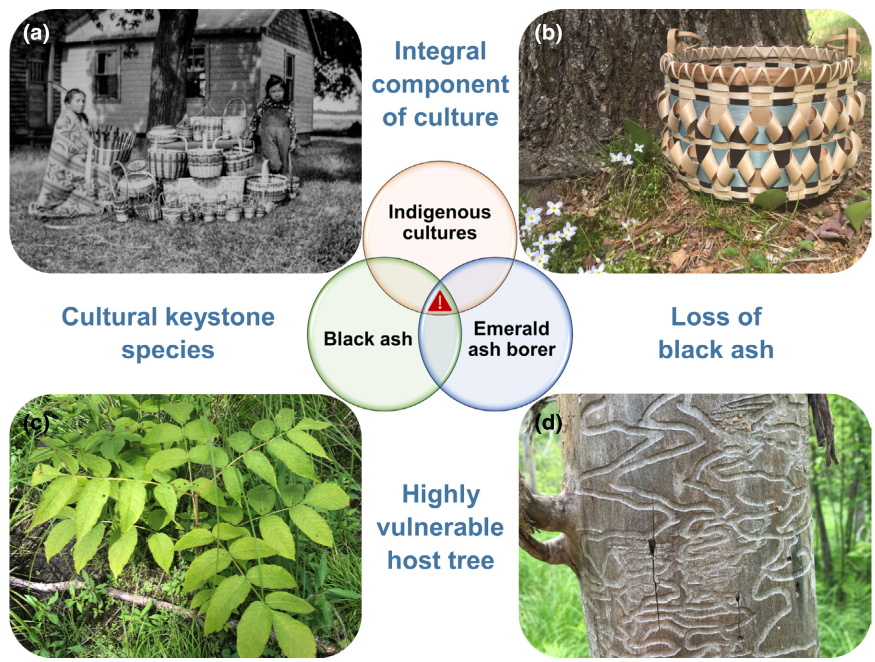

Figure 1. Black ash (*Fraxinus nigra*), a tree species at risk of functional extirpation by emerald ash borer (*Agrilus planipennis*), is an integral component of many Indigenous Tribal Nations and First Nations cultures in eastern North America. (a) Black ash basketmaking traditions have been shared in Tribal communities for generations. (b) A range of beautiful and utilitarian baskets are still created today by Indigenous artisans. (c) Black ash is a cultural keystone species and the preferred material for many traditional basketmakers; however, (d) it is highly vulnerable to the invasive emerald ash borer. Image credits: (a) R Church, Odawa/Pottawatomi; (b–d) NW Siegert.

black ash in the US and Canada. We then quantified the number of Tribal Nations and, using recent US census data, the proportion of Indigenous people with cultural associations to black ash who will likely be affected by projected EAB spread.

Methods

Investigating EAB spread over time

We compiled reports of initial detections of EAB in counties and civil divisions in the US and Canada, respectively, from 2002 to 2020 (CFIA 2022; EAB Info 2022) and used the regulated area as a proxy to draw inferences about spread and expansion of the EAB invasion in North America (hereafter, "spread"). Historical spread from the reconstructed epicenter (Siegert *et al.* 2014a) was evaluated in the cardinal and intercardinal directions by measuring geodesic distance to centroids of counties/civil divisions located at the edge of the contiguous regulated area each year. Potential differences among directions in spread rates of the primary population were examined with analysis of variance. Expansion of the area invaded by EAB was then modeled across the range of black ash at two different spread rates: (1) the average rate of spread observed from 2002 to 2020 and (2) a 50% reduced rate of spread to simulate potential effects of future management tactics and/or possible differences in EAB population dynamics in more northerly latitudes. Counties/civil divisions were considered infested once the modeled spread reached their centroid. Area invaded by EAB (observed and predicted) was compared to the native range of black ash (WebFigure 1) to estimate the percentage of range occupied over time. Increases in the percentage of the black ash range invaded by EAB over time were assessed through linear regression.

Assessing loss of basal area of black ash post-invasion

Estimates of black ash tree density and basal area (as derived from stems >2.5 cm diameter at breast height) were acquired from the US Forest Service Forest Inventory and Analysis Program (USFS FIA 2020) for two periods: inventories completed between 2003 and 2008 (earliest inventory period after the 2002 EAB detection in North America) and in 2019 (current). Changes in black ash resources were assessed in counties where the tree was present during the earliest inventory period. To determine how long a county was infested before total basal area losses of >25%, >50%, >75%, and >95% occurred, average percentage change in black ash basal area over the years since initial EAB detection in a county was calculated. Categorical, county-level losses of black ash basal area were then modeled as a function of EAB spread and length of time since the first EAB detection for the two spread rate scenarios.

Quantifying the Indigenous population potentially impacted

To assess potential cultural impacts of EAB invasion, we identified historically eastern-affiliated and federally recognized Tribal Nations linked to US states within the black ash range (USFS 2016), and then quantified the number and proportion of Tribal Nations associated with the current and projected EAB distribution. In addition, we used US census data (US Census Bureau 2021) to estimate the number of Native American individuals residing in US states where black ash occurs, and then determined the number and proportion of Indigenous people residing in counties infested by EAB currently and over time as EAB advances.

Results

Expanding EAB invasion jeopardizes black ash in North America

Spread of EAB from the reconstructed epicenter of the invasion in North America (Siegert *et al.* 2014a) between 2002 and 2020 averaged 48.5 ± 4.0 km yr^{-1} (range: 25.9–58.8 km yr^{-1}), and spread rates did not significantly differ by direction (F = 0.382; degrees of freedom = 7, 132; P = 0.911). Physical barriers, such as the Laurentian Great Lakes, and state regulatory decisions (eg county versus state quarantines) contributed to variability of spread rates but did not affect long-term directional trends. Area of the black ash range invaded by EAB has increased linearly since 2002 (r^2 = 0.98), with nearly 60% of the range occupied by 2020.

Results of directional spread analysis were used to inform models to project continued expansion of the EAB infested area. Two rates were modeled, including: (1) 50 km yr^{-1}, similar to the average rate of spread observed from 2002 to 2020; and (2) 25 km yr^{-1}, a rate selected a priori to reflect a 50% reduction in spread rate, which coincidently was similar to the minimum spread rate observed through 2020. Under the 50 km yr^{-1} spread scenario, the modeled EAB infestation expanded annually from 2021 to 2026, then sporadically before occupying 100% of the black ash range by 2031 (WebFigure 2). Similarly, under the 25 km yr^{-1} spread scenario, the EAB infestation steadily expanded annually from 2021 to 2030, then advanced sporadically before completely occupying the black ash range by 2042 (WebFigure 3). Model outputs suggested that more than 96% of the black ash range will be invaded by 2025 in the 50 km yr^{-1} spread scenario and by 2029 in the 25 km yr^{-1} spread scenario. In each scenario, the last portion of the black ash range to become invaded by EAB included portions of western Ontario; western Newfoundland; and Anticosti Island, Quebec, in the Gulf of St Lawrence.

Black ash density and basal area (stems >2.5 cm diameter) from Minnesota to Maine differed between the early

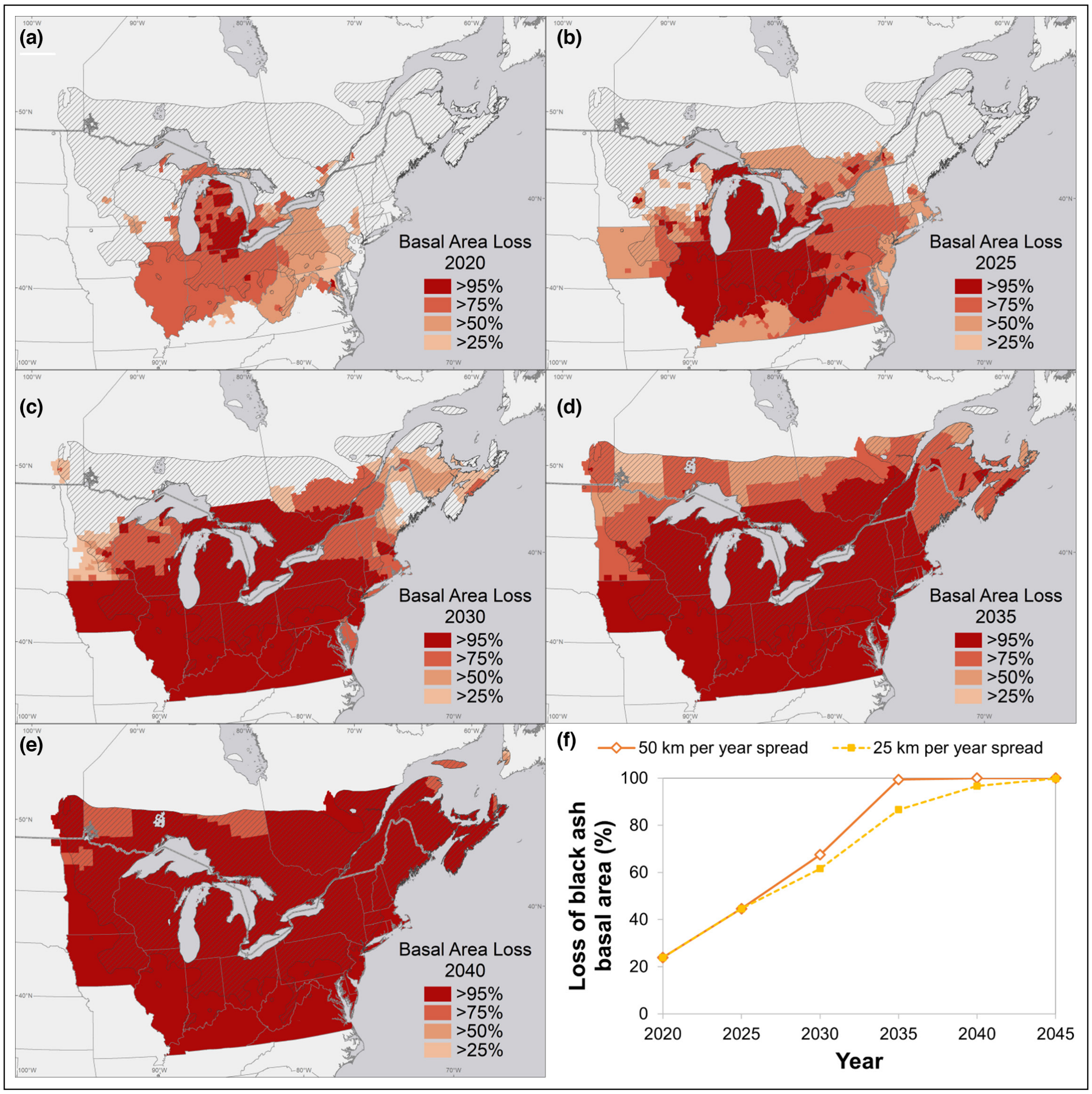

Figure 2. (a) Basal area losses of black ash in 2020 and (b–e) estimated losses at 5-year intervals through 2040 across the native range of black ash (crosshatch) at the current spread rate of about 50 km yr^{-1}. (f) Slowing the rate of spread by 50% mitigates basal area losses somewhat, although even reduced spread rate scenarios predict that much of the black ash resource will be negatively impacted by the emerald ash borer invasion over the next 20 years.

inventory period completed between 2003 and 2008, shortly after EAB was first detected in southeastern Michigan in 2002, and the most recent inventory in 2019 (WebFigure 4). Pronounced differences in black ash basal area within counties reflect the time interval between initial EAB detection and inventory completion. In counties infested for 0–4 years (n = 152), black ash basal area increased by an overall average of 88.7 ± 29.4% between the two inventories, although black ash basal area fell within 30% of those counties. In counties infested for 5–9 years (n = 52), increases in black ash basal area between inventories were lower, averaging 47.7 ± 31.5% overall, while 50% of the counties sustained reductions. Ten years after EAB detection within a county, however, black ash basal area notably decreased. In counties infested by EAB for 10–14 years (n = 51) and 15–17 years (n = 43), black ash basal area decreased on average by 65.5 ± 7.0% and 86.7 ± 6.5%, and reductions were sustained in 84% and 98% of the counties, respectively.

Basal area loss categories (ie >25%, >50%, >75%, and >95% total basal area loss) for model parameterization were informed using the average change in black ash basal area and years since EAB was first detected within counties. Specifically, basal area of black ash was reduced by 27.8 ± 24.2% (n = 11), 52.4 ± 16.6% (n = 9), 84.5 ± 6.8% (n = 10), and 99.2 ± 0.8% (n = 6) after 10 years, 11 years, 13 years, and 17 years of EAB infestation in a county, respectively.

Potential extirpation of cultural keystone species

Total basal area losses of black ash per county were modeled as a function of EAB spread and years post-EAB detection for both spread rate scenarios to estimate potential impacts to black ash resources across its native range in 5-year intervals. By 2020, >75% of total county-level black ash basal area across much of Michigan, Ohio, Indiana, Illinois, and the southern tip of Ontario is estimated to have been lost to EAB infestation (Figure 2a; WebFigure 5a). Under the 50 km yr^{-1} spread scenario, basal area losses occur rapidly across the range of black ash (Figure 2, b–e). Over the next 10 years and 15 years, >75% of black ash basal area is likely to be lost across 55.8% and 86.6% of its native range in the US and Canada, respectively. Under the 25 km yr^{-1} spread scenario (WebFigure 5), estimates improve only slightly; in the next 10 years and 15 years, >75% of black ash basal area is projected to be lost across 55.8% and 74.4% of its range in the US and Canada, respectively. However, in the percentage of the black ash range where >25% of basal area is projected to be lost, differences between the two spread scenarios were minor and short-lived (Figure 2f). Differences were most evident in 2035 but faded by 2040. We conclude that within 25 years, >95% of black ash basal area is likely to be lost across 99.8% and 96.4% of its range in the US and Canada in the 50 km yr^{-1} and 25 km yr^{-1} spread rate scenarios, respectively.

As of 2020, US data indicate that 39 of the 54 federally recognized Tribal Nations (72.2%) and 94% of the Native American population (>715,000 people) linked to states within the native range of black ash reside within the EAB-infested area (Figure 3). We estimate that the other 15 Tribal Nations and an additional 42,500 Native Americans live within the area that will be invaded by EAB by 2025 under the 50 km yr^{-1} spread scenario (Figure 4), or by 2029 under the 25 km yr^{-1} spread scenario (WebFigure 6). Nearly 711,000 Native Americans in states within the black ash range (>93%) reside in areas that are estimated to lose >75%

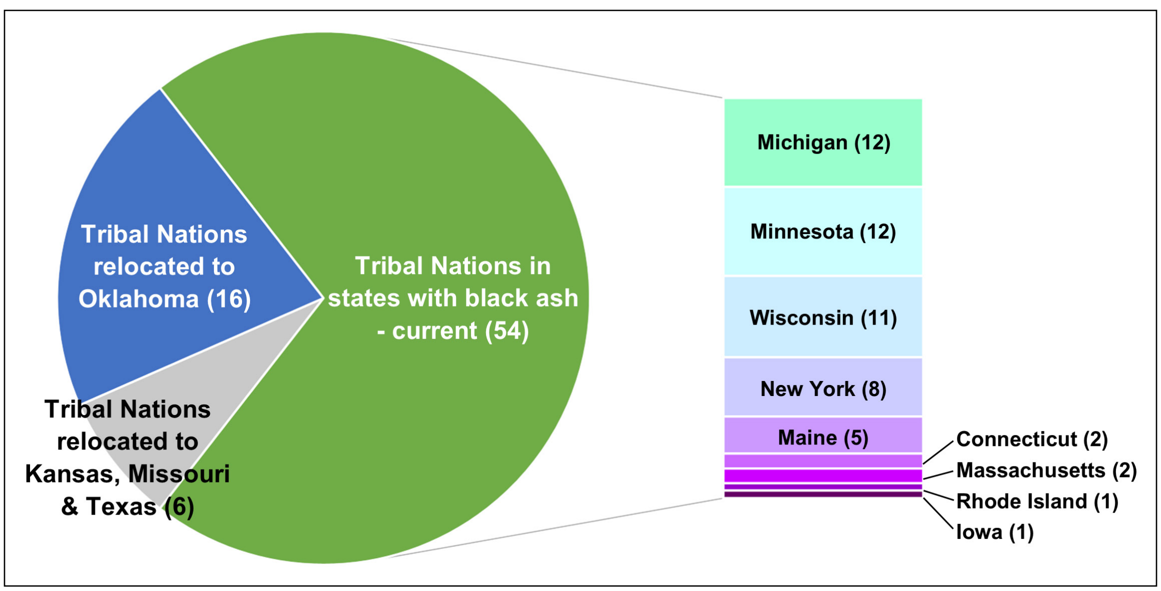

Figure 3. Of the 76 historically eastern-affiliated, federally recognized Tribal Nations in the US, 54 are presently located within nine states with a black ash resource (Michigan, Minnesota, Wisconsin, New York, Maine, Connecticut, Massachusetts, Rhode Island, and Iowa, as denoted in the callout bar to the right). The remaining 22 Tribal Nations were historically relocated to four states (Oklahoma, Kansas, Missouri, and Texas) without a black ash resource. Many additional non-federally recognized Bands or Tribal Nations are also located in these 13 states.

of the total black ash basal area by 2030 under either spread rate scenario. By 2035, >98% and >96% of the Native American population in those states will reside in areas where >75% of the black ash basal area is lost, under the 50 km yr^{-1} and 25 km yr^{-1} spread rate scenarios, respectively. By 2045, we estimate that >95% of the total black ash basal area will disappear due to EAB infestation across >96% of black ash range in the US and Canada, impacting virtually all Tribal Nations and First Nations peoples for whom black ash has cultural and spiritual importance.

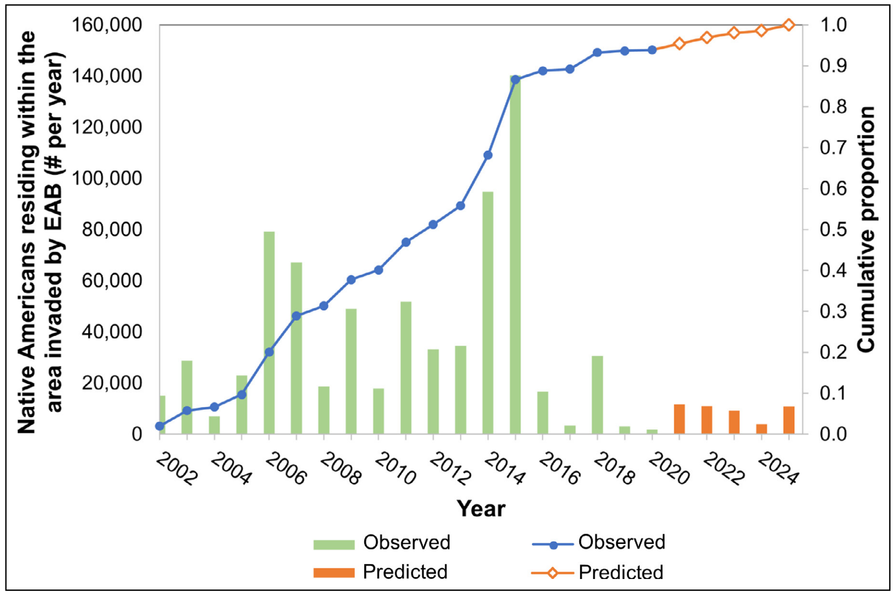

Figure 4. As of 2020, more than 94% of the Native American population living in states with a black ash resource resides within the area invaded by emerald ash borer. By 2025, models indicate that the invasion will likely encompass the remaining population.

Discussion

Ecological and economic impacts of EAB sustained in North America since its 2002 discovery already exceed those of any other invasive forest insect by orders of magnitude (Aukema *et al.* 2011). This is due in part to the abundance and broad distribution of ash across forested and urban settings, but also reflects the extraordinarily high rates of host mortality, particularly for highly preferred and vulnerable black ash and green ash (*Fraxinus pennsylvanica*) trees (McCullough 2019; Engelken and McCullough 2020; Siegert *et al.* 2021). Where vulnerable ash species comprise a substantial portion of the overstory, effects of EAB-related mortality cascade through the ecosystem, affecting species composition, structure and productivity of vegetation, and habitat for wildlife, as well as altering traits of adjacent waterways or wetlands (Klooster *et al.* 2018; McCullough 2019). Moreover, altered precipitation patterns that affect the extent or duration of flooding, shorter/warmer winters, or other effects of climate change (eg Kiefer *et al.* 2022) are likely to exacerbate impacts of EAB invasion, particularly in mature or overmature stands subject to other stressors (Palik *et al.* 2011).

Spread of EAB, initially facilitated by accidental transport of infested but non-symptomatic ash nursery trees, logs, or firewood (Cappaert *et al.* 2005), has been slowed by regulatory and extensive public outreach efforts. Despite the 2021 deregulation of EAB in the US, artificial spread of EAB seems likely to remain low. Infestations will continue to expand, however, due to natural dispersal, particularly by mature, mated females, which are capable of dispersing at least 800 m and probably >3 km (Mercader *et al.* 2015; Siegert *et al.* 2015).

Our results showed that county-level reductions in basal area of black ash, as evidenced by Forest Inventory and Analysis Program records (USFS FIA 2020), consistently lagged several years behind the first county report of EAB presence. This partially reflects the distance between black ash in inventory plots and locations where EAB was first detected, typically an urban, residential, or recreational area where visual symptoms of infestation are likely to be noticed (Poland and McCullough 2006). In addition, the lag between detection and loss of black ash basal area reflects growth of live overstory trees and saplings moving into larger size classes, along with EAB population dynamics. Ash trees, including black ash, can tolerate a low density of larvae and few external signs of infestation are apparent on most trees until ≥3–4 years after colonization (Cappaert *et al.* 2005; McCullough 2019). As larval densities increase over time, however, trees begin to decline and eventually succumb (Anulewicz *et al.* 2007; McCullough *et al.* 2019). Recent efforts to simulate EAB impacts in wetlands have included girdling every black ash in winter, then subsequently monitoring hydrology, regeneration, and other variables (Kolka *et al.* 2018; Palik *et al.* 2021), but the extent, timing, and scale of such abrupt mortality bears little resemblance to an actual EAB invasion. Even in sites dominated by vulnerable black ash trees, overstory mortality typically occurs over a period of at least 6–8 years (Siegert *et al.* 2021). Such temporal lags between initial EAB detection and black ash mortality are consistent with our analysis and use of EAB spread as a proxy to project eventual black ash basal area losses.

More research to assess ecological impacts of EAB in black ash forests is needed, and efforts to quantify social and cultural dimensions of EAB invasion on Indigenous peoples with traditional ties to black ash are notably scarce. Many Tribal Nations and First Nations peoples across the black ash range rely on these trees for traditional basketry, which may serve as the cultural identity for families within communities, as well as a source of income and prestigious acknowledgement. In addition to basketry, black ash is prominent in spiritual or ceremonial practices of some Tribal Nations, such as the Wabanaki, whose origin stories begin with a black ash tree. Efforts to sustain traditional cultural values and practices through recruitment and teaching of younger generations have been undertaken by many Tribal Nations and First Nations across the black ash range for decades.

Census data provide an estimate of how many Indigenous people currently reside on Tribal lands in the US, but this number greatly underestimates the potential impacts of widespread black ash mortality on Indigenous families. Members of many Tribal Nations that were relocated to other regions in the early 1800s retain strong cultural ties to black ash, despite their geographic separation or a lack of federal or state recognition of their Tribal Nation. Indigenous people and Tribal Nations without their own black ash resources must partner with managers of private or public lands to access and harvest trees for basketry or other purposes. In our experience, awareness of the cultural value of black ash varies considerably among resource managers.

Given the increasingly dire outlook for black ash in North America, comprehensive and collaborative efforts will be essential to prevent the functional extirpation of black ash and associated consequences for Indigenous cultures. Classical biocontrol involving release of EAB parasitoids native to Asia is underway in the 36 infested US states and five Canadian provinces (Duan *et al*. 2018), but the scale of these activities is small relative to the geographic range of black ash already invaded by EAB. Moreover, support for such releases varies considerably among Tribal Nations, and combined effects of introduced and native natural enemies have neither slowed EAB spread nor reduced ash mortality rates (Duan *et al*. 2018; McCullough 2019).

Other options may exist to conserve black ash and its role in Indigenous traditions at some level. Ahead of the EAB invasion, where harvests are permitted, basketmakers are stockpiling black ash by submerging logs, a practice that prevents decay while retaining traits necessary for weaving (Siegert *et al*. 2014b; Poland *et al*. 2015). Methods for freezing or drying partially processed splints that can be rehydrated also warrant consideration. Ongoing discussions among basketmakers include potentially using alternative materials to sustain traditional basketry practices such as Manchurian ash (*Fraxinus mandshurica*), an Asian species related to black ash but more resistant to EAB infestation (Tanis and McCullough 2016). Members of several Tribal Nations have participated in national or local efforts to collect and store seed from black ash populations to conserve genetic diversity prior to EAB invasion. In areas already invaded, some Tribal Nations are trunk-injecting a highly effective systemic insecticide (eg emamectin benzoate; Herms and McCullough 2014) into a few mature black ash trees to retain seed sources. Opportunities exist for combining this insecticide with girdling to create highly attractive but lethal EAB trap trees (McCullough *et al*. 2016). Such practices could benefit individual stands, while a comprehensive, area-wide approach (Mercader *et al*. 2015) could reduce EAB impacts on ecological processes and conserve black ash genetics at a broader scale, perhaps eventually providing opportunities for limited harvest by Indigenous basketmakers.

Our results show that over the next 20–25 years, the EAB invasion will encompass virtually the entire native range of black ash in North America. Ecological consequences seem likely to be wide-ranging and severe in black ash forests, with similarly profound cultural and socioeconomic impacts to Indigenous peoples. Innovative approaches, ideally combining traditional ecological knowledge, Indigenous practices, and Western science, will need to be developed to protect areas of black ash ahead of the EAB invasion and to restore remnants of this unique resource wherever possible.

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Data Availability Statement

Datasets utilized for this research were retrieved from the US Forest Service, Forest Inventory and Analysis Program Forest Inventory EVALIDator website (https://apps.fs.usda.gov/fiadb-api/evalidator), the US Census Bureau website (https://data.census.gov), the Canadian Food Inspection Agency website (https://inspection.canada.ca/plant-health/invasive-species/insects/emerald-ash-borer/eng/1337273882117/1337273975030), and the Emerald Ash Borer Information Network website (http://www.emeraldashborer.info).

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2654/suppinfo